Joint Management of Wildlife and Livestock Disease

**Richard D. Horan · Christopher A. Wolf ·
Eli P. Fenichel · Kenneth H. Mathews Jr.**

Abstract   We analyze a bioeconomic model of a multiple-host disease problem involving wildlife and livestock. The social planner's choices include targeted (i.e., infectious versus healthy) livestock harvests, non-targeted wildlife harvests, environmental habitat variables, and on-farm biosecurity to prevent cross-species contacts. The model is applied to bovine tuberculosis among Michigan white-tailed deer and cattle. We find optimal controls may target the livestock sector more stringently when the livestock sector exhibits low value relative to the wildlife sector. This is in contrast with the conventional wisdom on the issue that controls should primarily target wildlife species that serve as disease reservoirs.

Keywords   Bioeconomics · Infectious disease · Ecosystem management · White-tailed deer · Optimal control

1 Introduction

Livestock epizootics (the sudden spread of a disease in a non-human population) may threaten the economic well-being of farmers and ranchers, the food production system, valuable wildlife resources including game and endangered species, and human health (Cleaveland et al. 2001; Daszak et al. 2000). Epizootics in wildlife may pose similar threats (USDA-NASS 2002; TRS 2002). Indeed, the spread of infectious diseases among and between wild and domestic animals is a major global problem (Daszak et al. 2000; The Economist 2005). In

R. D. Horan (✉) · C. A. Wolf
Department of Agricultural Economics, Agriculture Hall, Michigan State University, East Lansing, MI 48824-1039, USA
e-mail: horan@msu.edu

E. P. Fenichel
Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA

K. H. Mathews Jr
Economic Research Service, USDA, 1800 M St., NWm, Washington, DC 20036, USA

this paper, we examine the management of a pathogen that infects both wild and domestic animals.

Solutions to disease problems might be straightforward if vaccinations were viable options or if the health status of individual animals was easily observable, enabling a cull of infected animals (albeit at a cost). But vaccination is not a practical option for many diseases, such as bovine tuberculosis (bTB) (*Mycobaterium bovis*) in cattle or deer, the focus of this paper (MDA 2002).[1] Moreover, health status is often unobservable prior to diagnostic testing (Lanfranchi et al. 2003), which is also the case for bTB. Livestock can often be tested for disease status to facilitate disease management, but postmortem testing is often the only practical option to identify wildlife health status (Lanfranchi et al. 2003). The result is that wildlife harvests are non-selective with respect to disease status, complicating wildlife disease control. This could have implications for managing disease among livestock populations. An inability to adequately control the disease in wildlife could result in the wildlife population exerting a continual force of infection on livestock, undermining livestock disease control efforts. This is particularly true for wildlife populations considered to be disease reservoirs for livestock—that is, when the wildlife population exerts the greatest influence on new infections in livestock.

Two approaches to wildlife disease control have been advocated when wildlife harvests are non-selective with respect to disease status. The first approach, which is only applicable when disease transmission is density-dependent, requires harvesting the aggregate population below an exogenous host-density threshold (Barlow 1991; McCallum et al. 2001). This is the population density level at which infectious contacts are sufficiently reduced that the disease begins to dissipate. Prolonged disease control can be costly when non-selective harvesting is the only management option or the host-density threshold occurs at a low-density.

The second approach is to manipulate environmental or habitat conditions to affect disease dynamics. Horan and Wolf (2005) analyzed a model of bTB in Michigan white-tailed deer (*Odocoileus virginianus*), where one type of habitat control, supplemental feeding of deer, artificially increased infectious contacts. As with harvests, supplemental feeding in their model is non-selective with respect to health status—healthy and sick deer have equal access to the feed. While there is no host-density threshold in their model (as they model density-independent or frequency-dependent disease transmission), there is a feeding threshold such that disease prevalence diminishes if feeding is kept below this value.[2] However, they found the maintaining feeding below this threshold so as to eradicate the disease might not be optimal: the benefits of maintaining sufficiently small feeding levels, in terms of reduced infectious contacts, may not outweigh the costs associated with reducing in situ reproduction of healthy deer.

A combination of harvests and habitat manipulation can be used to improve disease management when disease transmission is density-dependent. Fenichel and Horan (2007) develop a density-dependent model of bTB transmission in Michigan white-tailed deer,

---

[1] An approved vaccine for bTB does not currently exist in the United States. A vaccine does exist that reduces shedding of the organism but has failed to induce protection in a majority of field studies against natural infection (Hogarth et al. 2006). Even if it were approved, vaccinating cattle would mean that the only way to test true infections from vaccinated cattle would be post-mortem (Vordermeier et al. 2006). This means regions that vaccinate would not be considered bTB-free, and sanctions could ensue. For this reason, vaccines that are available and effective are not always used to inoculate livestock populations. With respect to deer, the vaccine, though not currently effective, may eventually be useful for slowing spread. It would, however, be expensive to administer and it would be difficult to identify previously vaccinated deer.

[2] Frequency-dependent transmission occurs when the contact rate is independent of host density—that is, a susceptible individual makes the same number of contacts with other animals regardless of the host population density (McCallum et al. 2001).

whereby prevalence can be managed via both harvests and habitat controls. They show that the host-density threshold becomes endogenous when habitat controls also influence transmission. Managers therefore do not simply manage the population relative to the threshold; rather, they manage both the population and the threshold. Fenichel and Horan (2007) find that prevalence rates are optimally reduced when two controls are used instead of a single control, but that eradication may still not be optimal.

A limitation of the bioeconomic work just described is that the biological component is a single-host-pathogen model. Only the wildlife population and disease dynamics are modeled explicitly, while livestock-sector impacts are captured implicitly through an exogenous damage function. Livestock population management or biosecurity choices that could influence damages by affecting disease transmission between wildlife and livestock were not explicitly modeled. Bicknell et al. (1999) model multiple populations in a bioeconomic model of bTB transmission between Australian brush-tailed possums and dairy cattle. But this was not truly a multi-host-pathogen model because no possum disease dynamics were modeled. Unlike standard disease models in which the transmission rate is a function of the infected population, Bicknell et al. modeled transmission from possums to cattle as proportional to the difference between the entire local possum population and an exogenous threshold.

The ecological literature has also focused primarily on single-host models. Dobson (2004), however, identified the development of multi-host models as a priority. A major focus of the emerging literature in this area is to identify the minimum amount of control effort required to eradicate the pathogen. Diekmann et al. (1990) derived the basic reproduction ratio for a pathogen (R_0) as a function of control effort, and showed how a constant (i.e., time-invariant) effort level could be chosen to eradicate the disease. Roberts and Heesterbeek (2003) criticized this approach because the control efforts would have to be administered uniformly across all hosts. They responded by deriving time-invariant, minimum control efforts that would need to be targeted to individual host populations to achieve eradication. The resulting management insights are of limited value, however, because they did not consider if disease eradication was a desirable objective, they did not recommend specific effort levels other than minimums, and the minimal efforts for one population were chosen independently of management applied to other hosts. Moreover, they did not consider the impacts of targeting non-reservoir hosts.

We expand the ecological literature on multi-host systems by recognizing that the economic and ecological systems are jointly-determined, and by considering economic and ecological tradeoffs when designing time-variant control strategies. A key result is that the host-density thresholds are endogenous, whereas the ecological literature treats them as exogenous (Dobson 2004; Roberts and Heesterbeek 2003). Even more importantly, we show that targeting controls towards host reservoir populations may be inefficient relative to controls such as biosecurity investments that can alter the reservoir status of these populations.

Our model also expands the bioeconomic literature. In contrast to Fenichel and Horan's (2007) single-host model, we find that the host-density thresholds in the multiple-host case are endogenous even under the conditions of a unitary vertical transmission rate and no feeding. The flexibility to manage the thresholds within one or both populations provides managers with improved targeting opportunities. This is important because the non-selective nature of wildlife harvest and habitat controls results in second-best management that may limit the optimal level of control. First-best solutions require controls that are selective according to health status, while non-selective controls create excessive control costs: for instance, unintended harvests of healthy animals impose costs on future generations, and reduced feeding

lowers the in situ productivity of both infected *and healthy* animals. Improved targeting reduces control costs, which provides incentives for greater control of the disease reservoir. However, we find that improved targeting (e.g. through biosecurity investment) also reduces damages, which creates an opposing incentive: reduce livestock-sector disease impacts so as to reduce the degree to which wildlife serve as a disease reservoir. Altering the wildlife population's status as a reservoir reduces the incentives for wildlife disease control, so that disease eradication is less likely to be optimal. The model and results presented here also expand the growing literature on managing multiple species in an bioeconomic system (e.g., Gutierrez and Regev 2005; Finnoff and Tschirhart 2003; Regev et al. 1998; Brock and Xepapadeas 2002).

These results are in contrast to conventional efforts to control epizootics transmitted among and between wild and domestic (livestock) populations. Standard approaches often involve attempts to eradicate all wildlife in an infected zone and depopulating infected livestock herds. Wildlife are often targeted first, with the primary motivation to protect livestock (particularly on small farms) (Leighton 2002). The wildlife-related benefits and costs from undertaking alternative disease control investments tend to be poorly understood and seldom considered.

2 Motivating Example

The models in this paper are based on the Michigan white-tailed deer example analyzed by Horan and Wolf (2005) and Fenichel and Horan (2007). The example allows for comparison with prior work. Moreover, several features of the problem facilitate the analysis. First, the infected deer population is considered closed within a four-county area in the northeastern part of the lower peninsula, known as deer management unit (DMU) 452 (Hicking 2002; Schmitt et al. 1997). Tracking studies indicate that DMU 452 deer migrate little (Garner 2001), and the Michigan Department of Natural Resources (MDNR) manages deer in DMU 452 as a unique population and estimates a low likelihood of spread (Hicking 2002).

Second, human-environmental interactions, in the form of supplemental feeding, play a major role in the problem. DMU 452 is the only known area in the United States where bTB has established in wild deer, and conventional wisdom held that the disease was not self-sustaining in wild deer populations (Hicking 2002). It is believed that area-specific features—particularly feeding programs that encourage deer to congregate—have enabled the disease to become endemic (Hicking 2002). Additionally, deer density in the region has been elevated about three and half times historic densities by feeding programs (O'Brien et al. 2002). The economic reason for providing this food is to boost natural productivity of the deer via an increase in the effective carrying capacity. But feeding also leads to increased transmission of the disease as deer congregate, and the supplementary food could also reduce disease-related mortality by supporting sick animals.

The disease has spread from deer to local livestock. Michigan lost its bTB accredited-free status in 2000 and was required to adopt a testing and control program for all cattle, goats, bison, and captive cervids. In addition, other states can bar imports of Michigan livestock at their discretion. Michigan received "split state" status for bTB in 2004, resulting in two disease management zones with separate requirements for animal movement, identification and testing. This status came about because extensive testing found the disease confined to the northeast corner of Michigan's lower peninsula, with regulatory costs now primarily confined to this area. Michigan agriculture supports culling deer to eradicate the disease. However, such extreme measures could be very costly, particularly since the cattle

sector is small (USDA-NASS 2002) and marginally profitable (Wittenberg and Black 2004) while deer hunting generates significant economic value in the infected region (Leefers et al. 1998).

3 A Multiple-host Model of bTB in Michigan Deer and Cattle

Consider a wildlife (deer) population, N_D, and a livestock (cattle) population, N_C, that inhabit a particular land area.[3] Deer-cattle contact is possible in the absence of biosecurity measures. Each population N_i ($i = C, D$) is partitioned into two health classes, $N_i = N_{iS} + N_{iI}$, where N_{iS} represents susceptible (healthy) animals and N_{iI} represents infected animals. Four processes affect the net growth of each sub-population N_{iz} ($i = C, D$; $z = S, I$): (i) net growth, G_{iz} (a measure of surplus production that combines birth and natural mortality processes), (ii) mortality due to the disease M_{iI} (which only applies to the infected population), (iii) new infections via transmission from population i to population j, T_{ij}, and (iv) harvests, h_{iz}.

First consider growth of the cattle population. As the cattle population is highly managed with frequent and accurate testing for infected animals, net growth of cattle is assumed to depend only on susceptible animals (i.e., $G_{CI} = 0$) and to take the linear form $G_{CS} = aN_{CS}$, where a is the net birth rate for cattle (Rosen et al. 1994; Foster and Burt 1992).[4]

While disease mortality does exist in cattle, we do not model it explicitly because we assume all cattle are tested and all test-positive cattle are removed before mortality can occur. There are two types of cattle harvests: market sales, h_{CS}, and disease-related harvests, h_{CI}, so that $h_C = h_{CS} + h_{CI}$. Ideally, market sales come from only the susceptible population while disease-related harvests come from only the infected population. This can be achieved with diagnostic testing, provided the tests are sufficiently accurate. Bicknell et al. (1999) show how to model testing errors (false positives and false negatives) in a bioeconomic framework. However, evidence from the Michigan case indicates that both types of errors are essentially zero (L. Judge Personal communication, 2006). This being the case, it is easily confirmed that testing all cattle and harvesting all test-positive cattle in each period (i.e., $h_{CI} = N_{CI}$) is optimal, provided testing and removal costs are sufficiently small—which we take to be the case (Wolf and Ferris 2000).

With all test-positive cattle removed in each period, we make some simplifying assumptions to model the number of infectious cattle. Each period starts with a wholly susceptible cattle stock, $N_{CS}^0 = N_C$, where the superscript "0" refers to the beginning of the period. Cattle are initially infected through deer-cattle transmission, which is modeled by the standard density-dependent transmission function (McCallum et al. 2001):

$$N_{CI}^0 = T_{DC} = (1 - \gamma K)\beta_{DC} N_C N_{DI} \tag{1}$$

where β_{DC} represents the rate at which healthy cattle acquire infection after contacting infectious deer. Here, infectious contacts are reduced by the level of biosecurity capital, K, which prevents inter-species contacts. The parameter γ indicates biosecurity effectiveness.

---

[3] The multiple-host problem is readily extendable to spatially explicit problems, because a metapopulation model is a special case of the multiple-host model.

[4] It is worth emphasizing here that we are modeling the social planner/policy-maker management decision with respect to the cattle population rather than farmer decisions. In the case of bTB, Michigan policy-makers attempt to control the disease in cattle by using quarantines, testing and slaughter—all of which can be carefully targeted and controlled.

The infectious cattle then re-infect the deer population

$$T_{CD} = (1 - \gamma K)\beta_{CD}N_{DS}N_{CI}^0, \tag{2}$$

and spread the disease in the cattle population in a similar manner as deer-cattle transmission (Bicknell et al. 1999), although K plays no role in this case[5]

$$T_{CC} = \beta_{CC}(N_C - N_{CI}^0)N_{CI}^0 \tag{3}$$

Here $N_C - N_{CI}^0$ represents the susceptible cattle stock after the initial infection. Given this specification, the total number of infected cattle that must be removed in each period is $h_{CI} = N_{CI} = (1 - \gamma K)\beta_{DC}N_C N_{DI}(1 + \beta_{CC}(N_C - (1 - \gamma K)\beta_{DC}N_C N_{DI}))$. Growth of the aggregate cattle population is

$$\dot{N}_C = aN_C - h_{CI} - h_{CS}. \tag{4}$$

The prevalence rate in cattle is N_{CI}/N_C, or

$$\theta_C = (1 - \gamma K)\beta_{DC}N_{DI}(1 + \beta_{CC}(N_C - (1 - \gamma K)\beta_{DC}N_C N_{DI})). \tag{5}$$

Neither h_{CS}, h_D, nor f (the biological control variables in our bioeconomic model below) affect the current value of θ_C, but they do affect future values of θ_C through the state variables.

Now consider the deer population. Growth of the deer populations takes the forms

$$\dot{N}_{DS} = G_{DS} - \sum_{j=D,C} T_{ji} - h_{DS} \tag{6}$$

$$\dot{N}_{DI} = G_{DI} - M_{DI} + \sum_{j=D,C} T_{ji} - h_{DI} \tag{7}$$

Following Horan and Wolf (2005), net growth of population N_{D_z} is given by the logistic growth function, $rN_{D_z}(1 - N_D/k)$, where r is the intrinsic growth rate and k is the carrying capacity. Underlying this specification is the assumption that fawns produced by infected deer also become infected, either *in utero* or after birth through maternal contact. Following Barlow (1991), the density-dependent component of the logistic equation, $(1 - N_D/k)$, depends on the aggregate population because susceptible and infected wildlife compete for the same habitat. We modify the density-dependent component by the impacts of supplemental feeding, denoted by f. Assume the effective carrying capacity is increased by feeding for $f < f^{max}$—at that point another resource becomes limiting. Denote the effective carrying capacity by $k/(1 - \tau f)$, where $\tau < 1/f^{max}$ is a parameter. Supplemental feeding increases the effective carrying capacity in a manner consistent with Walters (2001). As feeding is costly and only provides productivity benefits for $f < f^{max}$, f^{max} is an upper bound on feeding (this is made explicit in our simulation). Hence, net growth of population N_{D_z} is $G_{D_z} = rN_{D_z}[1 - (N_D/k)(1 - \tau f)]$.

For the infected population, net growth is reduced by disease-induced mortality. The disease mortality rate, in the absence of feeding programs, is denoted α. Supplemental feeding

---

[5] Technically, in a continuous-time model, cattle should become infected at one instant, and then in the next instant they should (i) spread of the disease back to deer, (ii) spread the disease to additional cattle, and (iii) be tested and removed. The current approach condenses all these processes into a single instant. This simplification reduces the number of state variables in the model while capturing all relevant processes. The primary implication is that the costs and benefits associated with processes (i)–(iii) are moved forward by one instant, which we do not believe introduces a significant error.

may decrease the effective mortality rate so that total disease mortality in deer is $M_{DI} = \alpha(1 - \chi f)N_{DI}$, where χ is a parameter.

Horizontal disease transmission (i.e., transmission not involving maternal contact) also alters a population after net growth has occurred. Cattle-deer transmission was defined in (2). For the deer-deer transmission, we adopt the standard density-dependent transmission function

$$T_{DD} = (1 + \omega f)\beta_{DD}N_{DS}N_{DI} \qquad (8)$$

where β_{DD} represents the rate at which healthy deer acquire infection after contacting infectious deer, and the parameter ω reflects the role of f on increasing infectious contacts. Cattle-to-deer transmission is analogous to deer-cattle transmission

$$T_{CD} = (1 - \gamma K)\beta_{CD}N_{DS}N_{CI}. \qquad (9)$$

Finally, harvests reduce the stock after net growth has occurred. Deer harvests are non-selective with regard to disease status: a manager can only choose the aggregate harvest, h_D. The harvest from health class z depends on the proportion of animals in health class z relative to the aggregate population N_D, such that $h_{Dz} = h_D N_{Dz}/N_D$.

It is more intuitive and mathematically convenient to work in terms of the variables N_D and θ_D instead of N_{DS} and N_{DI}, where $\theta_D = N_{DI}/N_D$ is the infected proportion of deer (the prevalence rate of the disease in deer). We note that $\dot{N}_D = \dot{N}_{DS} + \dot{N}_{DI}$ and $\dot{\theta}_D/\theta_D = \dot{N}_{DI}/N_{DI} - \dot{N}_D/N_D$. We rewrite Eqs. 6 and 7, fully specified, as

$$\dot{N}_D = rN_D(1 - (N_D/k)(1 - \tau f)) - \alpha(1 - \chi f)\theta_D N_D - h_D \qquad (10)$$

$$\dot{\theta}_D = \left[(1 + \omega f)\beta_{DD}N_D + \beta_{CD}(1 - \gamma K)N_C\theta_C/\theta_D - \alpha(1 - \chi f)\right]\theta_D(1 - \theta_D) \qquad (11)$$

None of the controls affects $\dot{\theta}_D$ directly, but they all do so indirectly through their effects on the state variables.

For given values of f and the state variables, the $\dot{\theta}_D = 0$ isocline can be solved for

$$\hat{N}_D = \Lambda_D(f, K, \theta_D, \theta_C, N_C) \qquad (12)$$

which represents a host-density threshold as a function of feeding, biosecurity capital, both prevalence rates, and the cattle population level. Disease prevalence is increasing ($\dot{\theta}_i > 0$) for values of $N_i > \hat{N}_i$, and prevalence is decreasing ($\dot{\theta}_i < 0$) for values of $N_i < \hat{N}_i$. Disease eradication results if $N_D < \hat{N}_D$ for long enough, but the threshold will vary over time as $\hat{N}_D$ endogenously depends on state and control variables. The threshold is decreasing in those variables that increase the net (of disease mortality) force of infection onto deer: when the force of infection is increased, $\dot{\theta}_D = 0$ is restored by diminishing the deer density to reduce infectious contacts and thereby generate an offsetting reduction in the force of infection. Alternatively, the threshold is increasing in those variables that reduce the force of infection onto deer: when the force of infection is reduced, $\dot{\theta}_D = 0$ is restored by increasing the deer density to generate an offsetting increase in the force of infection.

The threshold is decreasing in f because feeding increases infectious deer-to-deer contacts and reduces disease mortality. The threshold is also decreasing in θ_C and N_C, as increases in these variables increase the force of infection from cattle to deer. The threshold is increasing in K because more biosecurity results in fewer cross-species contacts. Finally, the threshold is also increasing in θ_D because, other things equal, a larger θ_D means that more infectious cattle-to-deer contacts are "wasted" on already-infected deer.

In contrast to a single-host version of this model, the host-density threshold is endogenous even in cases where feeding is not a choice variable. This is because harvests still directly influence the magnitude of population j and indirectly influence θ_i. But in a single-host model ($\beta_{ij} = 0$ for $i \neq j$) with no feeding ($f = 0$), the host-density that satisfies $\dot{\theta}_D = 0$ in Eq. 11 is $\hat{N}_D = \alpha/\beta_{DD}$, which is exogenous and fixed.

The endogenous, time-varying thresholds described by Eq. 12 also contrast with the ecological literature, which concentrates on threshold levels that arise at one particular state of the world—a pre-disease equilibrium that represents the point of disease invasion (Diekmann et al. 1990; Roberts and Heesterbeek 2003; Dobson 2004). Such thresholds are time-invariant and exogenously-fixed—independent of all other states (as these are held constant when the thresholds are derived). Moreover, the threshold-based control prescriptions that emerge from that literature only indicate a minimum amount of effort required to eradicate the disease, and do not indicate how to best target efforts differentially across host types or over time. In the following section, we construct a bioeconomic model to explore economically optimal management. Management strategies derived under this approach are chosen with consideration given to the full system dynamics and associated economic-ecological feedbacks.

4 A Bioeconomic Model

Suppose a social planner wishes to choose a population management and disease control strategy to maximize the discounted net benefits of deer hunting and cattle management. Traditionally, disease control in Michigan has focused on deer, with harvest and feeding levels being the primary control variables used by deer managers (Hicking 2002).[6] However, choices made in the cattle sector must also be considered, for economic damages to this sector depend on both deer management choices and the on-farm responses to the threat of cattle infection by deer.

We begin with the hunting sector. Hunters gain utility from the actual process of hunting deer and/or consuming meat and other deer products. Although harvests are non-selective, harvest values depend on health status because infected animals are identified through post-mortem testing (e.g., from lesions inside the carcass or examination of the tonsils), required in Michigan. The (constant) marginal utility from harvesting healthy deer is denoted p_D, which is not less than the (constant) marginal utility from harvesting infected deer, p_{DI}, i.e., $p_D \geq p_{DI}$. For simplicity, we set $p_{DI} = 0$ so that harvests of infected animals yield no benefits.[7] The benefits from hunting are therefore $p_D(1 - \theta_D)h_D$. Greater disease prevalence damages the hunting sector in terms of foregone harvest benefits. Assume harvests occur according to the Schaefer harvest function (see Conrad and Clark 1987), $h = qEN_D$, where E is hunting effort and q is the catchability coefficient. Assuming a unit cost of effort, c, total harvesting costs, restricted on the in situ stock, are $(c/q)h_D/N_D$. The unit cost of supplemental feed is assumed to be w.

Now consider the cattle sector. Healthy cattle have a (constant) marginal value of p_C, while infected cattle have no value (their carcasses are destroyed). The benefits from cattle sales therefore equal the revenue from cattle sales, $p_C h_{CS}$. The cost of maintaining the herd

---

[6] Michigan announced a goal of eradicating the disease by 2010. To that end, the wild white-tailed deer population in the area was to be decreased through increased sales of hunting licenses. In addition, the practice of legally feeding deer in the infected area was ended.

[7] The qualitative nature of the results would not be affected if instead $p_{DI} > 0$, provided that $p_D \geq p_{DI}$. However, setting $p_{DI} > 0$ would affect the trajectories in the numerical exercise. Fenichel and Horan (2007) explore this issue and find there is little impact.

is mN_C^2, where m is a parameter. We assume test-positive cattle are removed costlessly. Biosecurity investments Z are made at a constant cost of u. Capital accumulates according to the following equation of motion, where ζ represents depreciation:

$$\dot{K} = Z - \zeta K. \tag{13}$$

Given the discount rate ρ, an economically optimal allocation of harvests, feeding, biosecurity investments, and cattle stocking rates solves

$$\underset{h_D, h_{CS}, f, Z}{\text{Max}} SNB = \int_0^\infty [p_D(1-\theta_D)h_D + p_C h_{CS} - (c/q)h_D/N_D - wf - mN_C^2 - uZ]$$
$$\times e^{-\rho t} dt, \tag{14}$$

subject to the equations of motion (4), (10), (11), and (13), Eq. 5, the initial values of the state variables, N_{D0}, θ_{D0}, N_{C0} and K_0, and the feasibility conditions $h_D, I \geq 0, 0 \leq f \leq f^{max}$, and $K \leq 1/\gamma$.[8] The current value Hamiltonian is

$$H = p_D(1-\theta_D)h_D + p_C h_{CS} - (c/q)h_D/N_D - wf - mN_C^2 - uZ$$
$$+ \sum_{i=C,D} \lambda_i \dot{N}_i + \phi_D \dot{\theta}_D + \psi \dot{K} \tag{15}$$

where λ_i, ϕ_i and ψ are the co-state variables associated with N_i, θ_i and K, respectively.

The marginal impact of cattle sales on the Hamiltonian is

$$\partial H/\partial h_{CS} = p_C - \lambda_C. \tag{16}$$

The RHS of expression (16) is the linear coefficient of cattle sales in the Hamiltonian. Cattle sales should be as small as possible when $\partial H/\partial h_{CS} < 0$, and they should be as large as possible when $\partial H/\partial h_{CS} > 0$. A singular path for cattle sales should be followed whenever $\partial H/\partial h_{CS} = 0$.

The marginal impact of biosecurity investments on the Hamiltonian is given by

$$\partial H/\partial Z = -u + \psi. \tag{17}$$

If this expression is positive so that the marginal value of capital exceeds the marginal cost of investment, investments should be set at their maximum levels. If this expression is negative then $Z = 0$ is optimal. The singular solution is pursued when marginal investment costs and the marginal value of capital are equated. In this case, $\dot{\psi} = 0$ since u is fixed.

The marginal impact of deer harvests on the Hamiltonian is given by

$$\partial H/\partial h_D = p(1-\theta_D) - c/(qN_D) - \lambda_D. \tag{18}$$

The first two RHS terms represent the marginal rents from harvesting deer. As the harvests are non-selective, the marginal rents are decreasing in the prevalence rate. If the RHS of (18) is positive so that marginal rents exceed the marginal user cost, then harvests should be set at their maximum levels. No harvesting should occur if the RHS of (18) is negative. The singular solution is pursued when marginal rents and the marginal user cost are equated.

Now consider the marginal impacts of feeding on the Hamiltonian

$$\partial H/\partial f = -w + \lambda_D \partial \dot{N}_D/\partial f + \phi_D \partial \dot{\theta}_D/\partial f. \tag{19}$$

---

[8] Technically, the constraint on f should be $0 \leq f \leq \min\{f^{max}, 1/\chi\}$, but $f^{max} < 1/\chi$ in our numerical example. The feasibility conditions are explicit in our numerical example, though we do not model them here analytically.

The RHS of expression (19) is the linear coefficient of feeding in the Hamiltonian. The first RHS term is the marginal cost of providing supplemental feed. The second RHS term is the marginal benefit of feeding due to its role in increasing deer productivity. The third term, which is negative because $\phi_D < 0$ (i.e., greater disease prevalence reduces welfare, *ceteris paribus*), is the marginal cost of feeding due to its role of increasing disease prevalence. Specifically, increased feeding reduces the host-density threshold for deer, resulting in increased prevalence *ceteris paribus*. Hence, supplemental feeding can be viewed as an investment in both the productivity of deer stock and of the disease. This is because, like harvests, supplemental feeding is non-selective with respect to health status. If feeding were selective, then only healthy deer would be fed and the third RHS term would vanish.

If the RHS of expression (19) is positive, then feeding is optimally set at its maximum level, f^{max}. If the expression is negative, then $f = 0$ is optimal. The singular solution for f should be followed whenever the RHS of condition (19) vanishes, thereby equating the marginal benefits and marginal costs of feeding.

The conditions for an optimal solution also include four adjoint equations that must hold at each point in time.[9] These can be expressed as the following "golden rule" equations:

$$\rho = a + \left[-\left(\frac{\partial \theta_C}{\partial N_C} N_C + \theta_C \right) + \frac{\phi_D}{\lambda_C} \frac{\partial \dot{\theta}_D}{\partial N_C} \right] + \frac{\dot{\lambda}_C}{\lambda_C} - \frac{2m N_C}{\lambda_C} \tag{20}$$

$$\rho = \frac{\partial \dot{N}_D}{\partial N_D} + \left[\frac{\phi_D}{\lambda_D} \frac{\partial \dot{\theta}_D}{\partial N_D} - \frac{\lambda_C}{\lambda_D} \frac{\partial \theta_C}{\partial N_D} N_C \right] + \frac{\dot{\lambda}_D}{\lambda_D} + \frac{1}{\lambda_D} \frac{ch_D}{q N_D^2} \tag{21}$$

$$\rho = \frac{\lambda_D}{\phi_D} \frac{\partial \dot{N}_D}{\partial \theta_D} + \left[\frac{\partial \dot{\theta}_D}{\partial \theta_D} - \frac{\lambda_C}{\phi_D} \frac{\partial \theta_C}{\partial \theta_D} N_C \right] + \frac{\dot{\phi}_D}{\phi_D} - \frac{p_D h_D}{\phi_D} \tag{22}$$

$$\rho = -\frac{\lambda_C}{\psi} \frac{\partial \theta_C}{\partial K} N_C + \frac{\phi_D}{\psi} \frac{\partial \dot{\theta}_D}{\partial K} + \frac{\dot{\psi}}{\psi} - \zeta \tag{23}$$

Equation 20 equates the rate of return from holding cattle (the RHS) to its opportunity cost (ρ). The first RHS term is the marginal impact of cattle on reproduction. The second RHS term (in brackets) is the impact of more cattle on disease transmission in both populations: more cattle create more opportunities for within-species and cross-species infectious contacts. Alternatively, a larger cattle population has the adverse effect of reducing the host-density threshold for deer. This endogenous-threshold effect cannot arise in single-host models. The remaining RHS terms represent the additional benefits (i.e., capital gain) and maintenance costs of investing in a larger cattle population at the margin. Note that the term in brackets vanishes when there is no disease or when $K = 1/\gamma$, so that the resulting expression defines the optimal cattle stock in the absence of disease. When a disease is present, then the term in brackets is negative and reduces the rate of return to holding cattle. Other things equal, N_C must fall in the presence of disease in order to re-equilibrate the rate of return to ρ.

---

[9] The following condition is also necessary along a singular path associated with control variable $x (x = h_C,$ $h_D, f, Z)$ (Bryson and Ho 1975, p. 256): $(-1)^v \frac{\partial}{\partial x} \left[\left(\frac{\partial}{\partial t} \right)^{2v} \frac{\partial H}{\partial x} \right] \leq 0$, $v = 0, 1, 2, \dots$. This condition does not have an economic interpretation, and in the present model it can only be verified numerically. We have verified that this condition is satisfied throughout our numerical model. There are "no sufficient conditions for optimality of singular arcs" (Bryson and Ho 1975, p. 247). But see footnote 13 on the steps we took to verify the optimality of our solution.

Equation 21 equates the rate of return from holding deer (the RHS) to its opportunity cost (ρ). This equation has the same interpretation as Eq. 20, with two exceptions. First, an increase in the deer population increases cattle infections without affecting the host-density threshold for cattle. This is because our assumptions about immediately culling infected cattle eliminate the relevance of the threshold concept in cattle. Second, the final RHS term in (21) reflects a marginal cost savings (as opposed to an additional cost as in (20)) as harvesting costs are reduced for a larger deer stock. Finally, analogous to expression (20), the term in brackets vanishes when there is no disease so that the resulting expression defines the optimal deer stock in the absence of disease. When disease is present, then the term in brackets is negative and reduces the rate of return to holding deer. Other things equal, either N_D must fall or f must increase in the presence of a disease in order to re-equilibrate the rate of return to ρ.

Equation 22 is the adjoint condition associated with disease prevalence in deer. This condition equates the marginal benefit from investing elsewhere in the economy (ρ) to the marginal cost of re-directing resources away from disease control (the RHS). The first RHS term is the marginal impact of increased prevalence within deer on deer population growth. The second RHS term (in brackets) is the marginal impact of increased prevalence within deer on changes in disease prevalence within both populations: a larger prevalence within deer creates more opportunities for infectious within-species and cross-species contacts. An alternative way to view the cross-species term is as the marginal degree to which deer are a disease reservoir for cattle. The remaining RHS terms represent, respectively, the capital loss from having greater prevalence among deer, and marginal damages to hunters resulting from greater prevalence.

Finally, Eq. 23 equates the opportunity cost of capital (ρ) with the marginal benefits of employing capital as biosecurity (the RHS). The first RHS term is the marginal impact of biosecurity on reducing disease prevalence in cattle, achieved by reducing the degree to which deer are a disease reservoir for cattle. The second RHS term is the marginal impact of biosecurity on reducing disease prevalence in deer: more biosecurity reduces contacts between healthy deer and infected cattle, thereby increasing the host-density threshold for deer. The last two RHS terms represent the capital gains associated with biosecurity less depreciation.

The adjoint equations reflect the same tradeoffs as in the single-host case (e.g., Fenichel and Horan 2007), with three exceptions. First is the fact that there are now four states to manage (and hence four adjoint equations) as opposed to two in the single-host case without biosecurity. The second exception is the addition of the cross-host marginal effects in the current framework. The cross-host impacts on changes in deer prevalence are particularly important because these reflect how changes in the cattle population and in capital impact the host-density threshold for deer. The third difference is the effect of biosecurity on reducing the reservoir status of deer. These differences, relative to single-host models without biosecurity (which implicitly treat livestock management as fixed), yield more flexibility in controlling impacts of the disease. Here, management is no longer fixed, which reduces livestock-sector damages (as well as transmission back to deer) and eases the pressure to reduce prevalence in deer.

The optimal solutions for control variables in a linear control problem are feedback rules, with the optimal values at each point in time depending on the current state (Conrad and Clark 1987). The optimal feedback rules can involve various combinations of singular or non-singular controls, depending on the current state. A fully unconstrained, or quadruple-singular, solution is optimally pursued when (16)–(19) all vanish. Partial-singular solutions are optimal when exogenous constraints for one, two, or three control variables are binding

over some intervals of the optimal solution; that is, one, two, or three of the conditions (16)–(19) vanish. Partial-singular solutions arise within a blocked interval, a period of time when one or more of the controls is "blocked" or constrained from following the quadruple-singular path (Arrow 1968; Clark 1990). Finally, a fully constrained solution is pursued when all control variables are subject to binding constraints along an interval of the optimal solution.

With four control variables, there are too many combinations of potential partial and fully singular solutions to analytically derive each solution type here (see the Appendix for derivations of three types of partial singular solutions that arise in the numerical example). Moreover, the overall solution may involve a series of free and blocked intervals over time, with each interval corresponding to a different type of partial or fully singular solution. The potential combinations of possibilities render analytical analysis intractable, particularly since analysis of when to pursue blocked or free intervals is inherently numeric (Arrow 1968). We therefore examine the problem numerically.

5 Numerical Example

The data used to parameterize the model are provided in Table 1.[10] A common approach is to first analyze the fully unconstrained solution. However, given the parameterization in Table 1, we find that a fully unconstrained, or quadruple singular solution, does not exist for our numerical example. The first step is to figure out which variables, if any, should face a binding constraint at the initial values of the state variables.

5.1 Initial Choices for Supplemental Feeding and Biosecurity Capital

Fenichel and Horan (2007) find that f is initially constrained at f^{max} for the case in which there is no livestock-sector response to disease. Incorporating a livestock-sector response, as we do here, only reduces disease-related damages and further increases the incentives to feed. Indeed, in the extreme case with $K = 1/\gamma$ to eliminate cross-species transmission and hence livestock-sector damages, we find f is still initially constrained to f^{max}. Feeding represents an investment in deer productivity, enabling larger harvests even when the deer population is being reduced—which we show below is optimal.

We begin by setting $f = f^{max}$ and analyzing the partial singular solution associated with this case. The Appendix illustrates that the cattle population and biosecurity capital in this case are of the form $N_C(N_D, \theta_D)$ and $K(N_D, \theta_D)$, so that the problem can be analyzed in (N_D, θ_D) space. Given $f = f^{max}$, we find $K(N_{D0}, \theta_{D0}) = 75.5$, which is close to but less than the maximum level of $1/\gamma = 80$. A pulse investment to $K = 75.5$ is therefore optimal. Immediately after this initial investment, we find there are no incentives for additional biosecurity investment. This is because cattle prevalence begins to decline as a result of biosecurity, reducing cattle-sector damages and therefore any incentives for additional biosecurity investment. Moreover, there are incentives to immediately reduce the deer population (discussed below), which further reduces infectious cross-species contacts and the incentives for additional biosecurity investment. If we evaluate the optimal management path that arises when K is held fixed at 75.5 (described in detail below), we find that the marginal value of capital, as calculated from the optimized Hamiltonian, $(\partial H^*/\partial K|_{K=75.5})/\rho$ (see Rondeau

---

[10] Given the ongoing uncertainty and complexity associated with the Michigan bTB problem, the following analysis is best viewed as a numerical example that illustrates the economic intuition behind optimal disease management.

Table 1 Parameter values for numerical example

Parameter	Description	Value	Source (if different from Horan and Wolf 2005)[a]
N_{D0}	Initial deer population size	13,298	
θ_{D0}	Initial deer prevalence	0.023	
N_{C0}	Initial cattle population	2800	USDA-NASS (1996)
γ	Marginal impact of capital on cross-species transmission (=1/#farms)	1/80	USDA-NASS (1996)
r	Deer intrinsic growth rate	0.5703	
k	Deer carrying capacity	14,049	
τ	Marginal impact of feeding on k	8.0×10^{-5}	
f^{max}	Upper bound for feeding	10,000	
α	Disease induced mortality rate	0.3556	
χ	Marginal impact of feeding on α	5.32×10^{-5}	
β_{DD}	Deer–deer transmission coefficient	3.39×10^{-5}	Fenichel and Horan (2007)
ω	Marginal impact of feeding on β_{DD}	2.64×10^{-6}	
β_{DC}	Deer–cattle transmission coefficient	4.4×10^{-5}	Calibrated to generate cattle prevalence rate consistent with current estimates
β_{CD}	Cattle–deer transmission coefficient	4.4×10^{-5}	
β_{CC}	Cattle–cattle transmission coefficient	2.7×10^{-5}	USDA-NASS (1996)
a	Cattle growth rate	0.67	Bicknell et al. (1999)
p_D	Value of harvested healthy deer	1270.80	
c/q	Marginal harvesting cost	231,192	
w	Unit cost of feeding	36.53	
p_C	Value of harvested healthy cattle	770	Wittenberg and Black (2004) and Wittenberg and Wolf (2004)
m	Cattle maintenance cost parameter	0.225	Wittenberg and Black (2004) and Wittenberg and Wolf (2004)
u	Unit cost of biosecurity investment	28,500	British Columbia Ministry of Agriculture, Food and Fisheries (2002)
ζ	Biosecurity depreciation rate	0	Assumption
ρ	Discount rate	0.05	Assumption

[a] Values are derived based on data presented in the original sources. Where no source is provided, see Horan and Wolf (2005) for derivations and original sources

2001), is less than the unit cost of investment, u, along this entire path. This means that all investment in biosecurity occurs in the initial period.[11]

The biosecurity investment significantly reduces cross-species transmission, and this has implications for the adjoint conditions associated with the cattle and deer populations and deer prevalence. With respect to the cattle population, values of K close to $1/\gamma$ significantly reduce the bracketed term in condition (20). This reduces the incentives to adjust the cattle population in response to changes in bTB prevalence (particularly within the deer herd). With

---

[11] If investment costs were convex, then it becomes too costly to make all biosecurity investments in a single period. This also means that other controls (e.g., in the cattle or deer sectors) would become relatively cheaper, and substitution of these controls for biosecurity would occur.

respect to the deer population, values of K close to $1/\gamma$ significantly reduce the second term in brackets (the cross-species term) in condition (21). This reduces the incentives to adjust the deer population as a means of protecting the cattle population from disease. Finally, with respect to deer disease prevalence, values of K close to $1/\gamma$ significantly reduce the second term in brackets (the cross-species term) in condition (22). This means that the status of deer as a disease reservoir for cattle is significantly diminished, and as a consequence there are reduced incentives to invest in reducing θ_D (e.g., via reduced feeding or reduced deer population) as a means of protecting the cattle population from infection.

In sum, the large optimal value of K reduces feedbacks between the deer and cattle sectors. These feedbacks are not entirely eliminated, however, since the optimal value of K does not eliminate cross-species disease transmission. Eliminating cross-species disease externalities becomes exceedingly costly relative to other disease control activities and adaptation, and this result is consistent with the general notion that the marginal cost of eliminating an externality often exceeds the marginal benefit (Hanley et al. 1997). Still, as we indicate below, the cross-sector feedbacks are greatly diminished when $K = 75.5$, so that the two sectors are almost (though not entirely) managed independently.

The result of heavily targeting the cattle sector, via culls of infected cattle and biosecurity, to reduce cross-species transmission is in stark contrast to the more conventional policy recommendation of eradicating infected wildlife populations in order to protect livestock. The reason for our finding is that all deer-sector controls (harvesting and feeding) are non-selective, which makes the use of these controls particularly costly given that deer hunting is a highly valued activity in this region (Leefers et al. 1998). In contrast, cattle-sector controls are selective, which makes the use of these controls particularly inexpensive given that the cattle sector in this region is not very profitable (Wittenberg and Black 2004).

5.2 The Deer Sector: Management When Feeding and Biosecurity Investment are Constrained

Biosecurity capital is fixed along the entire optimal path, and feeding is initially constrained to $f = f^{max}$. The constraint on feeding is only temporary, as the complete solution involves moving across different types of partial singular solutions—each of which can be viewed as a sub-path. However, as two of the sub-paths involve constraints on feeding, it is informative to first describe the dynamics for these constrained cases prior to discussing the complete solution. We also note that, though optimal outcomes for the deer and cattle sectors are jointly-determined, optimal values of N_C and h_C are of the form $N_C(N_D, \theta_D)$ and $h_C(N_D, \theta_D)$ (see Appendix). Our discussion therefore centers on deer-sector dynamics in (N_D, θ_D) space.

First consider the partial singular solution when $Z = 0$ (with $K = 75.5$) and $f = f^{max}$. The phase plane is presented in Fig. 1a. The darkened line with the arrows represents the separatrices (the partial singular solution) leading to a saddle point steady state at C. Starting at point A, the optimal solution is a pulse harvest to jump to the separatrix at point B, and then follow the separatrix to the steady state.[12] The separatrix is followed, as opposed to moving directly to the steady state along a most rapid approach path (as is common in many

---

[12] The optimality of this strategy can be shown using the approach outlined by Mesterton-Gibbons (1987) and also used by Fenichel and Horan (2007). We briefly outline the arguments here (see those other papers for details, which are straightforward but somewhat tedious). With K and f fixed, the singular solution for h is a feedback rule $h_D(N_D, \theta_D)$ (see Appendix). As this feedback rule is feasible over much of the state space (N_D, θ_D), different singular paths arise for different initial states. All of these paths, except the separatrix, lead away from the interior steady state to outcomes where the optimality conditions are eventually violated.
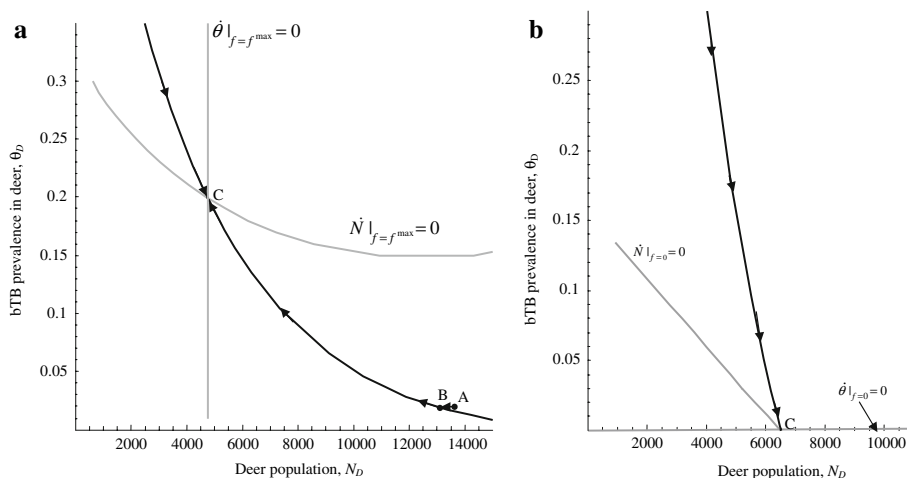
Fig. 1 Optimal management when (**a**) $f = f^{max}$, and (**b**) $f = 0$

autonomous, linear resource problems; Clark 1990), due to the second-best nature of the problem. Specifically, the use of non-selective controls creates adjustment costs that lead to slower adjustment. This feature arises even when f is not constrained.

Along the separatrix, θ_D increases while N_D falls. θ_D rises along the separatrix because reductions in N_D reduce the rate of return to reducing disease prevalence. This is particularly true since it is costly to reduce θ_D when f is fixed at $f = f^{max}$. Rather, the rate of return condition (22) is satisfied by allowing θ_D to increase. In contrast, N_D falls along the separatrix because increases in θ_D reduce the return to holding deer in situ (see condition (21)). The rate of return condition (21) is satisfied by reducing N_D, which increases the marginal growth of the deer population, all else equal. Eventually a steady state is achieved at point C. However, moving to the steady state is only optimal if $f = f^{max}$ remains optimal everywhere along this solution path. We show below that $f = f^{max}$ does not remain optimal. Prior to reaching the steady state, the system moves into a region of the state space where f is no longer constrained.

Next consider the partial singular solution when $Z = 0$ (with $K = 75.5$) and $f = 0$. The phase plane is presented in Fig. 1b. The darkened line with the arrows represents the separatrix leading to a saddle point steady state at C, at which the disease is eradicated. As with Fig. 1a, the optimal solution is a pulse harvest to the separatrix (the partial singular solution), and then following the separatrix, to the steady state C. The economic intuition is the opposite of the case of Fig. 1a: the return from reducing θ_D is high, particularly since f is constrained to $f = 0$. These reductions in θ_D in turn increase the rate of return to holding deer in situ, creating incentives to grow the deer population. Of course, moving to the steady state is only optimal if $f = 0$ remains optimal everywhere along this solution path, but we show below that $f = 0$ does not remain optimal along the separatrix. Prior to reaching the steady state, the system moves into a region of the state space where f is no longer constrained.


Footnote 12 continued
The separatrix is the lone path that always satisfies the necessary conditions for optimality, and so the pulse harvest to this path is required.

Fig. 2 Deer sector phase plane for the numerical example

5.3 The Deer Sector: The Complete Solution

The complete numerical solution for managing the deer sector is presented in Fig. 2.[13] The phase plane is partitioned into three sections. The section to the right of the $f = f^{max}$ boundary is the relevant portion of the phase plane from Fig. 1a (for the partial singular solution in which $Z = 0$ and $f = f^{max}$). The section to the left of the $f = 0$ boundary is the relevant portion of the phase plane from Fig. 1b (for the partial singular solution in which $Z = 0$ and $f = 0$). There is no equilibrium in either of these constrained regions.

The central region between the $f = 0$ and $f = f^{max}$ boundaries represents the phase plane for the partial singular solution in which only Z is fixed (i.e., when the solution is singular with respect to the controls: deer harvests, feeding, and cattle sales). We denote this as the triple singular solution. The isoclines for the triple singular solution intersect in the interior of the central region. This intersection defines an equilibrium at the point $N_D = 6890$ and $\theta_D = 0.076$. The eigenvalues of the differential equation system, linearized at the equilibrium point, are complex with positive real parts. This indicates that the equilibrium is an unstable focus (Conrad and Clark 1987). It is only optimal to be at this point if the system starts at this point. Otherwise, it is optimal to spiral away from this point. The $f = 0$ and $f = f^{max}$ boundaries are defined by the loci of points for which values of f in the triple singular solution become constrained at $f(N_D, \theta_D) = 0$ and $f(N_D, \theta_D) = f^{max}$, respectively.

---

[13] We have taken a number of steps to verify the optimality of this solution. First, we examined the optimality of the optimal control solution by numerically evaluating welfare along alternative paths. For instance, we considered a variety of alternative paths that would have moved the system either more quickly or more slowly from the initial point to the $f = f^{max}$ curve, while also satisfying the necessary conditions. We also evaluated jumps directly to the cycle in the central region or directly to the $f = 0$ curve. We did the same sort of exercise each time there was movement from one "type" of solution to another. In each case, the plan in Fig. 2 was optimal. Second, we developed a discrete-time approximation of the model and solved it using math programming (in AD Model Builder, Otter Research). We found the resulting outcome to be qualitatively the same and numerically very similar to the one presented in Fig. 2. Because the optimal control specification allows us to solve for the exact feedback rules, facilitates economic interpretations, and is more amenable to phase plane analysis, we have based our numerical analysis on the optimal control results.

Fig. 3 Time paths of optimally managed deer and cattle populations (points of reference A–D correspond to Fig. 2)
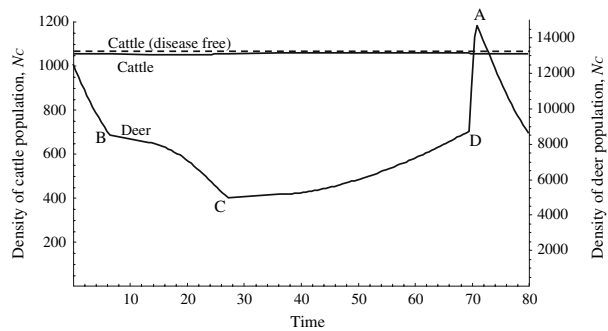
Management is initiated at the initial state values N_{D0} and θ_{D0}, represented by point A in Fig. 2. After the pulse investment to $K = 75.5$, $f = f^{max}$ remains optimal as none of the other states has changed, and as the reduction in cross-species infections only results in greater incentives to feed. An optimal plan is to jump to the separatrix in the $f = f^{max}$ region (as in Fig. 1a) and then follow that singular arc until intersecting the $f = f^{max}$ boundary. Once at the $f = f^{max}$ boundary, the phase dynamics from the adjoining isosectors result in the optimal path traveling up the $f = f^{max}$ boundary before moving into the central region. The optimal trajectory then moves into the northeast quadrant of the central region. Deer density, N_D, continues to fall while θ_D continues to increase along this interior path. The incentives driving this movement are the same as those that had driven the movement along the separatrix, though the incentives for allowing θ_D to increase are diminished as $f(N_D, \theta_D)$ declines below f^{max}. The reduction in f substitutes for population controls in managing θ_D, increasing the rate of return to disease control. In turn, the slower increases in θ_D diminish the incentives to further reduce N_D, though this is offset somewhat by the smaller feeding levels which reduce the rate of return to holding deer in situ. The result is that the state variables move more slowly in the interior isosector than they did along the separatrix where $f = f^{max}$. This can be seen in Fig. 3 for the deer population.

The optimal path begins to rotate around the focus point to intersect the $\dot{\theta}_D = 0$ isocline. At this point, θ_D has reached a critical level such that there are now sufficient incentives to reduce θ_D. The value of N_D that coincides with the $\dot{\theta}_D = 0$ isocline is the *optimal* host-density threshold. Along an optimal path, the relation for the host-density threshold in Eq. 12 becomes $N_D = \Lambda_D (f(N_D, \theta_D), K^*, \theta_D, \theta_C(N_D, \theta_D), N_C(N_D, \theta_D))$. This expression can be re-solved for the *optimal* host density threshold $N_D = \tilde{N}_D(\theta_D, K^*)$, which reflects both ecological and economic considerations. In particular, the value of f on this curve is smaller for smaller values of θ_D and larger values of N_D, reflecting the control the manager has over the threshold as well as the tradeoffs the manager makes between feeding and population controls. At higher prevalence rates, the manager prefers to reduce prevalence through population controls. This is because population controls have a greater marginal impact on transmission when prevalence is high. Moreover, by allowing larger rates of supplemental feeding, greater harvest levels are required to reduce the population and this generates greater harvesting benefits. At lower prevalence rates, population controls have little marginal impact on reducing transmission and so reducing feeding becomes the preferred approach to further reducing prevalence.

The optimal path crosses the $\dot{\theta}_D = 0$ isocline and moves southwesterly. Although θ_D falls, which increases the rate of return to holding deer, the further reductions in feeding along this path more than offsets this effect and N_D continues to fall. The optimal path eventually

intersects the $f = 0$ boundary. Note that the separatrix associated with the $f = 0$ case crosses the $f = 0$ boundary above where the optimal path intersects the boundary. This means the separatrix lies to the right of the $f = 0$ boundary in the locale of the intersection and below, so that a jump to the $f = 0$ boundary would be optimal for any point to the left of the boundary. Hence, the phase arrows in the relevant portion of the $f = 0$ region point towards the boundary. The result is that the optimal path is pushed down the $f = 0$ boundary.

The path eventually re-emerges into the central region, indicating that it is optimal to re-introduce supplemental feeding to further increase deer productivity. Prevalence is decreasing along this path while the deer population is increasing. The incentives driving this movement are the same as those that had driven the movement along the separatrix in Fig. 1b, though the incentives for decreasing θ_D are diminished as f is increased above zero. In turn, this reduces the incentives for increasing N_D relative to what would have occurred along the separatrix.

The optimal path cycles around the focus point and eventually crosses the host-density threshold. At this point, prevalence has fallen to such low levels that the rate of return to disease control is reduced to the point that it becomes optimal to allow θ_D to increase, driven by increases in both N_D and f. Feeding is increased as it represents an investment in deer productivity, increasing the population while enabling larger harvests along the singular path. The optimal path eventually intersects the $f = f^{max}$ boundary, at which point it becomes optimal to moves as quickly as possible to the separatrix within the $f = f^{max}$ region. This requires forgoing deer harvests for a brief period. The cycle begins again and continues.

The solution is qualitatively similar to Horan and Wolf's (2005) and Fenichel and Horan's (2007) solutions, except that optimal prevalence rates are much larger in the present solution. For instance, the largest prevalence rate along the current path is more than five times larger than the largest rate in the solution to those other models. The larger rates in the present model arise because marginal damages to the cattle sector are small due to biosecurity investment, whereas marginal damages to the cattle industry were assumed to be positive and constant in Horan and Wolf's and Fenichel and Horan's models.
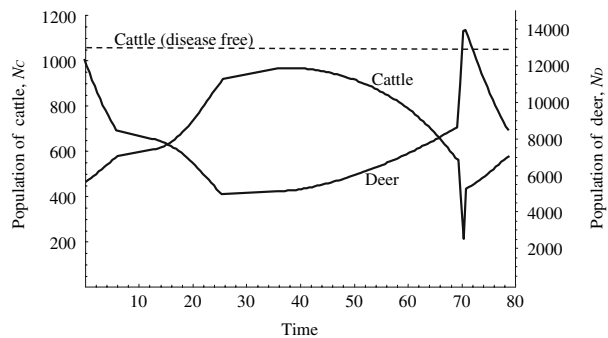
5.4 The Cattle Sector

The optimal time-path of the cattle stock is illustrated in Fig. 3. After an initial "bang-bang" adjustment, the optimal level of cattle is almost constant and only slightly below the level that would arise in the absence of deer-cattle transmission, i.e., the constant singular value of N_C that solves the following golden rule derived from (16) and (20) when $K = 1/\gamma$

$$\rho = a - 2mN_C/p_C. \tag{24}$$

The level in Fig. 3 is not constant, but dips only slightly when the deer population or the deer prevalence rate are at their highest levels. The cattle sector exhibits virtually no response to changes in the deer sector. Moreover, since cattle-sector disease damages are small due to the large biosecurity investment, the cattle sector has very little impact on management in the deer sector (this is verified by solving the model with $K = 1/\gamma$). For all intents and purposes, the two sectors are managed separately once the large biosecurity investment has been made.

Fig. 4 Time paths of deer and cattle for the base case model with no biosecurity

6 Sensitivity Analysis

We now consider the sensitivity of results to changes in the model parameters. To conserve on space we focus on two scenarios: an increase in the cattle price (so that the cattle sector is more valuable) and a restriction on biosecurity investments. The results for changes in other parameters are qualitatively similar to those reported in Fenichel and Horan's (2007) sensitivity analysis, and so we do not devote space to those scenarios here.

First, consider an increase in the cattle price, p_C, when there are no restrictions on biosecurity investments. This increased price increases optimal cattle stocks. With little or no risk from infection, condition (24) suggests that the cattle stock increases in proportion to the price increase. Together, the price increase and the increased cattle stock increase the marginal value of biosecurity investments, resulting in more investment and even fewer infectious contacts within the cattle sector. A 32% or greater increase in p_C relative to the base case results in maximum biosecurity investment, $K = 1/\gamma$.

Now consider restrictions on the use of biosecurity. Specifically, suppose no biosecurity capital is available. The results for the base case parameters indicate that management of the deer sector is minimally affected. Rather, controls are shifted from biosecurity investments to reductions in the cattle stock during periods of high risk. The time paths of the deer and cattle stocks are shown in Fig. 4 to be inversely correlated. The cattle population hovers close to its no-disease value (given by Eq. 24) when the deer population is low, as this corresponds to low deer-to-cattle and cattle-to-deer transmission. However, the cattle stock is reduced by approximately 60% when the deer population is at its highest levels, corresponding to periods of high risk which reduce cattle-sector returns (see Eq. 20). The reduction in cattle also help to lower deer prevalence, as targeted reductions in the cattle population reduce the "force of infection" from cattle to deer.

Finally, consider the combination of no biosecurity and a ten-fold increase in cattle prices, representing a situation in which cattle are much more highly valued relative to deer. In this case the cattle population is essentially constant at its no-disease value (given by Eq. 24). Virtually all controls in this case occur in the deer sector due to the fact that cattle are now significantly more valuable than deer. The results for the deer sector are illustrated in Fig. 5. Deer populations and prevalence rates are significantly reduced (relative to the path in Fig. 2) along the optimal cycle due to increased harvesting and reduced feeding levels, even though both of these are non-selective controls. In particular, the lower portion of the cycle turns up prior to hitting the f^{max} boundary as feeding is reduced relative to the base case scenario in Fig. 2, and the cycle bends backward more quickly as harvests are increased relative to the base case. These adjustments are made to "protect" the more valuable cattle sector.
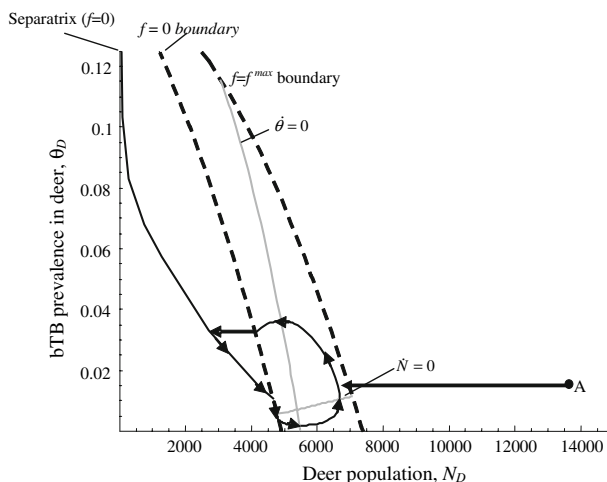
Fig. 5 Deer-prevalence dynamics when cattle are ten times more valuable

7 Conclusions

Recommendations for managing animal diseases have tended to focus on disease eradication as the primary objective. To this end, the "rule of thumb" in the ecological literature is that reservoir host populations need to be managed relative to a host-density threshold. Yet, the analytical basis for these recommendations treats a host's reservoir status and host-density threshold as fixed. Moreover, these recommendations have ignored economic tradeoffs, even though disease management is inherently an economic problem due to the costs and benefits associated with reducing disease prevalence.

This paper is one of a series that investigates the application of economics to diseases involving wildlife and livestock (Bicknell et al. 1999; Horan and Wolf 2005; Fenichel and Horan 2007). Two themes have emerged from this bioeconomic literature. First, as is a common result in bioeconomic models, the ecological and economic systems are jointly determined. In a single-host model, Fenichel and Horan (2007) showed the host-density threshold to be an endogenous function of economic choices, under certain circumstances. In the present multiple-host framework, we found the endogeneity of host-density thresholds to be a more general result due to the species' (ecological) interactions. We also found it is possible to alter the degree to which a species is a disease reservoir, by investing in biosecurity to reduce cross-species transmission.

The second theme in the bioeconomic literature is how to target resources to best manage a disease outbreak. In many wildlife settings, controls cannot be targeted selectively across infected and susceptible populations—they are non-selective with respect to disease status. This generally reduces the efficiency of wildlife controls. Horan and Wolf (2005) and Fenichel and Horan (2007) discuss tradeoffs in targeting non-selective population and habitat controls (i.e., supplemental feeding) in a single-host model and find that disease eradication is not optimal, though having several control options can improve welfare and lead to lower disease prevalence (Fenichel and Horan 2007). Bicknell et al. (1999) discuss the targeting of controls across wildlife and livestock species when wildlife serve as a disease reservoir for livestock and when livestock and wildlife controls can be targeted selectively. They find a mix of livestock and wildlife controls is optimal, but that efforts to suppress the wildlife reservoir

are the most effective at reducing prevalence. We also find that controls should primarily be directed at reducing the reservoir status of wildlife, but the types of controls and the ultimate impact on disease outcomes differ. Bicknell et al. (1999) found population control efforts should be used to suppress the wildlife reservoir, but this result is at least partially driven by the ability to selectively harvest diseased wildlife in their model. We found population controls to be a comparatively costly approach due to the expense associated with them being non-selective with respect to disease status. Rather, we find that significant on-farm biosecurity investments are warranted to reduce wildlife disease status, due to biosecurity being a highly targeted control for reducing cross-species transmission. The result is that wildlife impose fewer externalities on the livestock sector and so there are fewer incentives to directly control the disease in wildlife—the opposite of what Bicknell et al. (1999) found and in contrast to the conventional focus on eradication. These results support the notion that the ability to target controls that will be effective in managing disease transmission is crucial for determining an optimal disease strategy.

In whole, this body of work on the economics to diseases involving wildlife and livestock demonstrates the need to consider the endogenous nature of ecological relations and associated management tradeoffs, including the ecosystem services and damages provided by hosts and their pathogens. Managers need to consider how well alternative strategies target the services (damages) they wish to manage relative the cost of those strategies. Moreover, it should be recognized that improving social welfare may not coincide with pathogen reduction. All too often, the goal of pathogen eradication is promoted irrespective of the costs and without due consideration given to mitigation as an alternative strategy that may be pursued.

Appendix

Here we illustrate the derivation of the three partial singular solutions that arise in the numerical example. A fully unconstrained, or quadruple singular solution, can also be derived analytically, but this solution does not exist in our numerical example (i.e., interior values do not simultaneously arise for all relevant variables) and so we do not devote space to it. In each case, the basic approach is outlined in Bryson and Ho (1975, Chapter 8), though a fundamental difference between our model and the examples they present is that Bryson and Ho do not include discounting, which leaves them with the additional necessary condition that the value of their Hamiltonian is optimally constant over time.

Partial Singular Solution When Only f is Constrained

The singular solution in this case involves constraining f to either $f = 0$ or $f = f^{max}$, and also setting conditions (16)–(18), but *not* (19) equal to zero to derive the optimality conditions $\lambda_C = p_C$, $\psi = u$, and $\lambda_D = p(1 - \theta_D) - c/(qN_D)$. First, take time derivatives of the conditions $\lambda_C = p_C$ and $\psi = u$ to derive $d\lambda_C/dt = d\psi/dt = 0$. These optimal values for λ_C, ψ, $d\lambda_C/dt$, and $d\psi/dt$ can be substituted into the arbitrage conditions (20) and (23), which can then be solved for $K(N_D, \theta_D, \phi_D)$ and $N_C(N_D, \theta_D, \phi_D)$. These relations represent the optimal values of capital and cattle, respectively, conditional on the values of the remaining state and co-state variables.

Now take the time derivative of the condition $\lambda_D = p(1 - \theta_D) - c/(qN_D)$ and substitute the resulting expression for $\dot{\lambda}_D$, along with the optimal values for λ_C, $K(N_D, \theta_D, \phi_D)$ and $N_C(N_D, \theta_D, \phi_D)$, into condition (21). Upon doing this, condition (21) can be written in implicit form as $\rho = \Omega(N_D, \theta_D, \phi_D, f)$ (note that h_D drops out of this expression, as is

typical in renewable resource problems that are linear in the harvest; see Clark 1990). Next solve this relation for $\phi_D(N_D, \theta_D, f)$. Finally, take the time derivative of $\phi_D(N_D, \theta_D, f)$ and substitute the resulting expression in for $\dot{\phi}$ (along with the solutions for all other variables) in condition (22). It is possible to solve for $h_D(N_D, \theta_D, f)$, which represents a feedback rule for deer harvests. Also, given $\phi_D(N_D, \theta_D, f)$, it is possible to solve for $N_C(N_D, \theta_D, f)$. The optimal feedback rules for capital investment and net cattle sales are then $Z = dK(N_D, \theta_D, f)/dt + \zeta K$ (for $Z \geq 0$ only) and $h_{CS} = dN_C(N_D, \theta_D, f)/dt - [aN_C - h_{CI}]$.

Partial Singular Solution When Only Z is Constrained

The singular solution in this case involves constraining Z to $Z = 0$ (so that K is fixed), and setting conditions (16), (18), and (19), but *not* (17) equal to zero to derive the optimality conditions $\lambda_C = p_C$, $\lambda_D = p(1 - \theta_D) - c/(qN_D)$, and $\phi_D = (w - [p(1 - \theta_D) - c/(qN_D)]\partial \dot{N}_D/\partial f)/\partial \dot{\theta}_D/\partial f$. First, take the time derivative of the condition $\lambda_C = p_C$ to derive $d\lambda_C/dt = 0$. The optimal values for λ_C, ϕ_D, and $d\lambda_C/dt$ can be substituted into the arbitrage condition (20), which can then be solved for $N_C(N_D, \theta_D, K)$ and the associated feedback rule for net cattle sales $h_{CS} = dN_C(N_D, \theta_D, K)/dt - [aN_C - h_{CI}]$.

Now take the time derivatives of the conditions $\lambda_D = p(1 - \theta_D) - c/(qN_D)$ and $\phi_D = (w - [p(1 - \theta_D) - c/(qN_D)]\partial \dot{N}_D/\partial f)/\partial \dot{\theta}_D/\partial f$ and substitute the resulting expressions for $\dot{\lambda}_D$ and $\dot{\phi}_D$, along with the optimal values for λ_C, ϕ_D, and $N_C(N_D, \theta_D, K)$, into conditions (21) and (22). After doing this, conditions (21) and (22) can be solved simultaneously for the feedback rules $h_D(N_D, \theta_D, K)$ and $f(N_D, \theta_D, K)$.

Partial Singular Solution When f and Z are Constrained

The singular solution in this case involves constraining f to either $f = 0$ or $f = f^{max}$, constraining Z to $Z = 0$ (so that K is fixed), and also setting condition (16) and (18) equal to zero to derive the optimality conditions $\lambda_C = p_C$ and $\lambda_D = p(1 - \theta_D) - c/(qN_D)$. First, take the time derivative of the condition $\lambda_C = p_C$ to derive $d\lambda_C/dt = 0$. The optimal values for λ_C and $d\lambda_C/dt$ can be substituted into the arbitrage condition (20), which can then be solved for $N_C(N_D, \theta_D, \phi_D, K)$.

Now take the time derivative of the condition $\lambda_D = p(1 - \theta_D) - c/(qN_D)$ and substitute the resulting expression for $\dot{\lambda}_D$, along with the optimal values for λ_C, and $N_C(N_D, \theta_D, \phi_D, K)$ into condition (21). Upon doing this, condition (21) can be written in implicit form as $\rho = \Omega(N_D, \theta_D, \phi_D, K, f)$ (as above, h_D drops out of this expression). Next solve this relation for $\phi_D(N_D, \theta_D, K, f)$. Take the time derivative of $\phi_D(N_D, \theta_D, K, f)$ and substitute the resulting expression in for $\dot{\phi}$ (along with the solutions for all other variables) in condition (22). It is possible to solve for $h_D(N_D, \theta_D, K, f)$, which represents a feedback rule for deer harvests. Also, given $\phi_D(N_D, \theta_D, K, f)$, it is possible to solve for $N_C(N_D, \theta_D, K, f)$. The optimal feedback rule for net cattle sales is then $h_{CS} = dN_C(N_D, \theta_D, K, f)/dt - [aN_C - h_{CI}]$.

References

Arrow KJ (1968) Optimal capital policy with irreversible investment. In: Wolfe JN (ed) Value, capital, and growth: papers in honour of Sir John Hicks. University Press Edinburgh, Edinburgh

Barlow N (1991) A spatially aggregated disease/host model for bovine tb in New Zealand possum populations. J Appl Ecol 28:777–793

Bicknell KB, Wilen JE, Howitt RE (1999) Public policy and private incentives for livestock disease control. Aust J Agric Resour Econ 43:501–521

British Columbia Ministry of Agriculture, Food and Fisheries (2002) Fencing factsheet: deer farm perimeter fence

Brock W, Xepapadeas A (2002) Optimal ecosystem management when species compete for limiting resources. J Environ Econ Manage 44:189–220

Bryson AE Jr, Ho YC (1975) Applied optimal control: optimization, estimation, and control. Hemisphere Publishing, New York

Clark CW (1990) Mathematical bioeconomics. Wiley, New York

Cleaveland S, Laurenson MK, Taylor LH (2001) Disease of humans and their domestic mammals: pathogen characteristics, host range and the risk of emergence. Philos Trans Roy Soc Lond Ser B 356:991–9

Conrad JW, Clark CW (1987) Natural resource economics: notes and problems. Cambridge University Press, New York

Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife-threats to biodiversity and human health. Science 287:443–449

Diekmann O, Heesterbeek JAP, Metz JAJ (1990) On the definition and computation of the basic reproduction ratio R_0 in models of infectious disease in heterogeneous populations. J Math Biol 28:365–382

Dobson A (2004) Population dynamics of pathogens with multiple hosts species. Am Nat 164:s64–s78

Fenichel EP, Horan RD (2007) Jointly-determined thresholds and economic tradeoffs in wildlife disease management. Nat Resour Model 20:511–547

Finnoff D, Tschirhart J (2003) Harvesting in an eight species ecosystem. J Environ Econ Manage 45:589–611

Foster K, Burt O (1992) A dynamic model of investment in the US beef cattle industry. J Bus Econ Stat 10:419–426

Garner MS (2001) Movement patterns and behavior at winter feeding and fall baiting stations in a population of white-tailed deer infected with bovine tuberculosis in the northeastern lower peninsula of Michigan. Ph.D. Dissertation, Michigan State University, East Lansing

Gutierrez AP, Regev U (2005) The bioeconomics of tritrophic systems: applications to invasive species. Ecol Econ 52:383–396

Hanley N, Shogren JF, White B (1997) Environmental economics: in theory and practice. Oxford University Press, New York

Hicking GJ (2002) Dynamics of bovine tuberculosis in wild white-tailed deer in Michigan, Michigan Department of Natural Resources Wildlife Division Report No. 3363

Horan RD, Wolf CA (2005) The economics of managing infectious wildlife disease. Am J Agric Econ 87: 537–551

Hogarth PJ, Hewinson RG, Vordermeier HM (2006) Development of vaccines against bovine tuberculosis. J Pharm Pharmacol 58:749–757

Lanfranchi P, Ferroglio E, Poglayen G, Guberti V (2003) Wildlife vaccination, conservation and public health. Vet Res Commun 27:567–574

Leefers L, Ferris J, Propst D (1998) Economic consequences associated with bovine tuberculosis in northeastern Michigan. A report to the Michigan Departments of Agriculture, Natural Resources, and Community Health

Leighton F (2002) Foreign animal diseases and Canadian wildlife: reasons for concern and the elements of preparedness. Can Vet J 43:265–267

McCallum H, Barlow N, Hone J (2001) How should pathogen transmission be modelled?. Trends Ecol Evol 16:295–300

Mesterton-Gibbons M (1987) On the optimal policy for combined harvesting of independent species. Nat Resour Model 2:109–134

Michigan Department of Agriculture (MDA), Michigan Bovine TB, http://www.bovinetb.com (downloaded August 21, 2002)

O'Brien DJ, Schmitt SM, Fierke JS, Hogle SA, Winterstein SR, Cooley TM, Moritz WE, Diegel KL, Fitzgerald SD, Berrry DE, Kaneene JB (2002) Epidemiology of *Mycobacterium bovis* in free-ranging white-tailed deer in Michigan. Prev Vet Med 54:47–63

Otter Research. An introduction to AD model builder, version 7.0, for use in nonlinear modeling and statistics. Otter Research, Ltd, Nanaimo

Regev U, Gutierrez AP, Schreiber SJ, Zilberman D (1998) Biological and economics foundations of renewable resource exploitation. Ecol Econ 26:227–242

Roberts MG, Heesterbeek JAP (2003) A new method for estimating the effort required to control an infectious disease. Proc Roy Soc Lond B 270:1359–1364

Rondeau D (2001) Along the way back from the brink. J Environ Econ Manage 42:156–182

Rosen S, Murphy KM, Scheinkman JM (1994) Cattle cycles. J Polit Econ 102:468–492

The Economist (2005, Nov. 19). Infection: the usual suspects, pp 96–97

The Royal Society (2002) Infectious diseases in livestock: scientific questions relating to the transmission, prevention and control of epidemic outbreaks of infectious disease in livestock in Great Britain. London

Schmitt SM, Fitzgerald SD, Cooley TM, Bruning-Fann CS, Sullivan L, Perrry D, Carlson T, Minnis RB, Payeur JB, Sikarskie J (1997) Bovine tuberculosis in free-ranging white-tailed deer in Michigan. J Wildl Dis 33:749–758

U.S. Department of Agriculture, Animal and Plant Health Inspection Service (USDA-APHIS). Foot-and-mouth disease, http://www.aphis.usda.gov/oa/pubs/fsfmd301.htm January 2002 (downloaded August 30 2002)

U.S. Department of Agriculture, Animal and Plant Health Inspection Service (USDA-APHIS) (1996) Appendix C: simulation model of tuberculosis risk to cattle from infection in free-ranging white-tailed deer, assessing the risks associated with M. Bovis in Michigan free-ranging white-tailed deer. Center for Animal Disease Information and Analysis (CADIA) Technical Report No. 01–96

U.S. Department of Agriculture, National Agricultural Statistics Service (USDA-NASS) (2002) Census of agriculture

Vordermeier HM, Chambers MA, Buddle BM, Pollock JM, Hewinson RG (2006) Progress in the development of vaccines and diagnostic reagents to control tuberculosis in cattle. Vet J 171:229–244

Walters S (2001) Landscape pattern and productivity effects on source-sink dynamics of deer populations. Ecol Modell 143:17–32

Wittenberg E, Black J (2004) Feeder steer business analysis summary. Michigan State University Agricultural Economics Staff Paper 05–15. November 2005

Wittenberg E, Wolf C (2004) Michigan dairy farm business analysis summary. Michigan State University Agricultural Economics Staff Paper 05–10. October 2005

Wolf CA, Ferris JN (2000) Economic consequences of bovine tuberculosis for Michigan livestock agriculture. A report to the Michigan Department of Agriculture